Chapter A6: Fish Population Modeling and the § 316(b) Benefits Case Studies

Predicting the long-term consequences of impingement and entrainment (I&E) for the populations of affected fish species requires some form of population modeling. However, because of the many uncertainties associated with population modeling, the use of fish population models to assess CWIS impacts remains a topic of ongoing debate. While this debate has many interesting dimensions, this chapter focuses only on fish population modeling as it relates to the benefits case studies. Section A6-1 introduces the general reader to concepts of population regulation that are relevant to population modeling and summarizes key features of fish stock-recruitment models, a class of models advocated by some industry groups for § 316(b) impact assessments. Section A6-2 discusses the use

of stock-recruitment models in fisheries management, and Section A6-3 discusses how such models have been applied to evaluate potential CWIS impacts on fish populations. Section A6-4 discusses some of the uncertainties associated with stock-recruitment models that may limit their utility in a regulatory context. Finally, Section A6-5 discusses EPA's decision to adopt a "precautionary approach" in evaluating the biological impacts of cooling water intake structures (CWISs).

A6-1 BACKGROUND

A6-1.1 Population Regulation

The growth of biological populations is limited by natural regulatory factors such as environmental variation, random changes in rates of survival or reproduction, predator-prey relationships, disease, and competitive interactions with other individuals (Begon and Mortimer, 1986). Factors that result in population changes that are unrelated to population size are known as density independent factors. Examples include climatic variables such as temperature, floods, droughts, etc. Factors that can influence populations in relation to the size of the population, such as competition, predation or disease, are referred to as density dependent factors. The population size to which a population will tend to return in response to density dependent regulation is known as the equilibrium population.

The concept of density dependence is fundamental to the study of biological populations and to the application of population modeling in fisheries management. Compensation refers to the theoretical ability of a population to offset (compensate for) increased mortality (Goodyear, 1980; Rose et al., 2001). According to the theory of compensation, populations will grow when population density is low and will decline when density is high because competition and other density dependent processes will increase or decline in relation to population size. In this way, populations size remains relatively stable.

Inverse density dependence, or depensation, can occur when demographic rates (e.g., birth rates, survival rates) decrease at low densities (Liermann and Hilborn, 2001). Depensation can occur because of a failure to find mates when a population contains few individuals, or when fish harvest rates, impingement and entrainment, or other sources of mortality remain constant even though the population is depressed. Depensation tends to destabilize populations.

While considered likely to operate in most biological populations, compensation and other density dependent processes are difficult to observe and measure. When modeling population dynamics, this makes it difficult to identify underlying mechanisms of density dependent response and to estimate the magnitude and direction of population changes.

A6-1.2 Fish Stock-Recruitment Models

Fish stock-recruitment models are based on the assumption that some form of density dependent compensation will help maintain a stable population size despite losses of adults due to fishing (Getz and Haight, 1989; Ricker, 1975; Rothschild, 1986; Hilborn and Walters, 1992; Quinn and Deriso, 1999). Different functional forms of the stock-recruitment relationship represent different hypotheses about the response of recruitment to changes in the density of the spawning stock. There are three basic hypothetical stock-recruitment relationships, a density independent relationship, the Beverton-Holt curve, and the Ricker curve, as described below.

Density Independent Model. In the absence of any density dependent effect, it is assumed that there is a strictly linear relationship between stock and recruitment (Figure A6-1).

Figure A6-1: A Density Independent Relationship between Spawning Stock and Recruitment
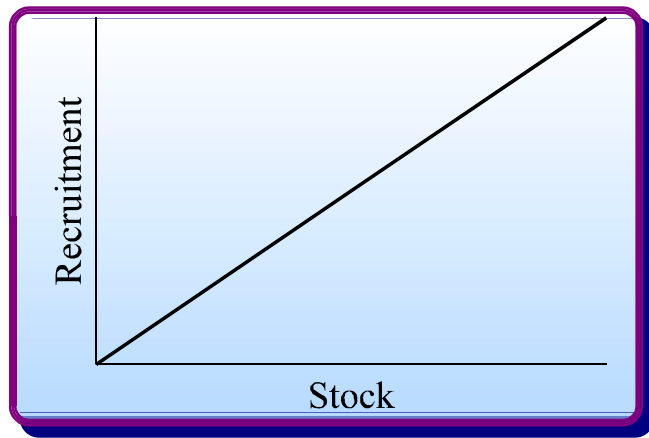
This density independent relationship between stock and recruitment changes if recruitment is influenced by the number of spawners (i.e., if recruitment is density dependent). There are two general types of density dependent compensation modeled by stock-recruitment curves, the Beverton-Holt and the Ricker models.

Beverton-Holt Model. The Beverton-Holt model (Getz and Haight, 1989) depicts density dependent recruitment of a resource limited population in which resources are not shared equally. It is considered most appropriate for modeling populations characterized by within cohort cannibalism or resource competition (Wootton, 1990; Hilborn and Walters, 1992). According to the Beverton-Holt formulation, a population consists of "winners" or "losers" — each individual receives some of the available resources, or not. This means that as resources such as spawning sites become fully utilized, further increases in population size will not result in additional recruits, and when spawner abundance is reduced, there is reduced recruitment. This is expressed in the Beverton-Holt formulation as:

$R = 1 / \beta + \alpha/P$

where:

R = recruits
P = parent stock
α and β = fitted parameters

The parameters α and β are fit to field data and define the shape of the stock-recruitment curve. The slope α is considered an indication of the population's maximum reproductive rate and β represents compensatory mortality as a function of stock size. According to the Beverton-Holt model, recruitment increases in relation to stock size up to an asymptote, or maximum, at high stock abundance (Figure A6-2).

Figure A6-2: The Beverton-Holt Stock-Recruitment
Relationship
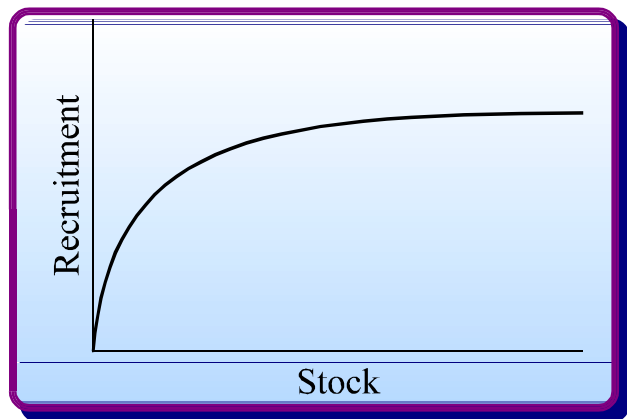
Ricker Model. In contrast to the Beverton-Holt stock-recruitment model, the Ricker model (Ricker, 1975) predicts declining recruitment at high stock levels according to the equation:

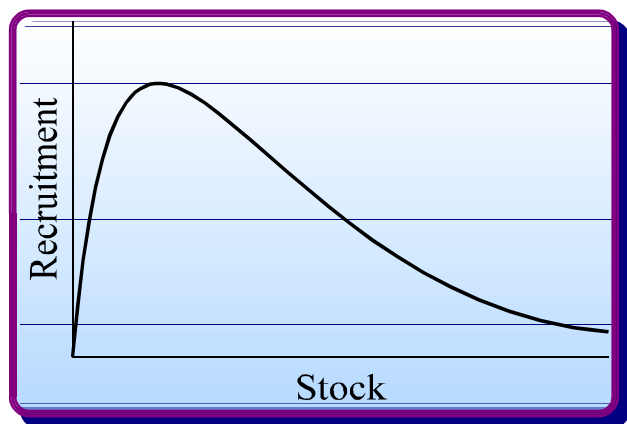$$R = \alpha P^{-\beta P}$$

where, as for the Beverton-Holt model:

R = recruits
P = parent stock
α and β = fitted parameters

According to the Ricker model, the exponential term $(-\beta P)$ gives the density dependent effect of parent stock on recruitment and α is the slope of the curve when P is small (Figure A6-3).

Figure A6-3: The Ricker Stock-Recruitment Relationship

The assumption of the Ricker model is that resources are divided equally among individuals in a population. As a consequence, as density increases all members of the population receive an increasingly smaller amount of available food or other resource. The result is that at very high densities, very few individuals will survive to reproduce. Therefore, according to the Ricker equation, recruitment is controlled by αP when parent stock is small, and R increases with P in a density-independent fashion. However, when parent stock is large, R is controlled more by the density dependent term $-\beta P$, and the number of recruits declines as stock increases. The Ricker relationship is expected when there is cannibalism of the young by adults or resource competition between parents and progeny, resulting in poor survival of young at high stock sizes (Wootton, 1990; Hilborn and Walters, 1992).

A6-2 USE OF STOCK-RECRUITMENT MODELS IN FISHERIES MANAGEMENT

Stock-recruitment models and their underlying assumptions about compensation are applied in fisheries management to estimate how much fishing mortality can be sustained on a long term basis by a commercially harvested fish population (Rothschild, 1986; Hilborn and Walters, 1992; Quinn and Deriso, 1999). This involves estimating the population's potential surplus production and compensatory reserve, as discussed below.

Surplus Production. Surplus production refers to the number of recruits produced above that needed for replacement at a given stock level and is considered the production available for harvesting (Getz and Haight, 1989; Ricker, 1975; Gulland, 1974). Surplus production is estimated by fitting stock-recruitment curves to empirical fisheries data. The 45 degree line from the origin of the stock-recruitment curve depicts exact replenishment of the population, and the area of the curve above the replacement line is the production that is available to the fishery (see Figure A6-4). The steeper the initial slope (α) of the stock-recruitment curve, the greater the expected compensatory response of the population to density changes and the larger the harvestable portion of the stock. In Figure A6-4, Population A has the strongest compensatory response. As the slope decreases, the compensatory response is less, as in Population B. As the curve approximates a straight line, the density dependent response is considered to be very weak, resulting in what is known as undercompensation, as seen in Population C.

Figure A6-4: Hypothetical Stock-Recruitment Curves
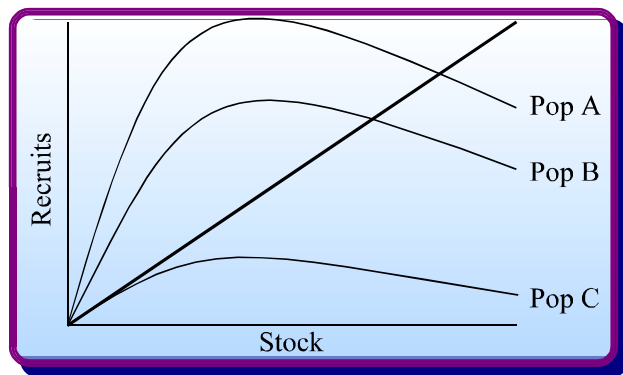
Compensatory Reserve. The slope of the spawner-recruit curve near the origin, where compensation effects are small, indicates the population's maximum reproductive rate. This gives an indication of the compensatory reserve, or the capacity of the population to offset any form of increased mortality (Myers et al., 1999; Rose et al., 2001). This is expressed as:

$$R = \alpha S\, f\,(S)$$

where:

R   = recruits
α = the slope at the origin
S   = spawners
f (S)   = the relationship between survival and spawner abundance

A difficulty in estimating compensatory reserve is that there are rarely data on abundance at very low population sizes (i.e., near the origin of the spawner-recruit curve) (Myers et al., 1999; Rose et al., 2001). As a result, one of the major uncertainties in fisheries management is the actual magnitude of compensatory reserve in any given population.

A6-3 USE OF STOCK-RECRUITMENT MODELS TO EVALUATE CWIS IMPACTS

To evaluate CWIS impacts on fish populations, stock-recruitment models have been modified to consider entrainment mortality of young instead of harvesting of adults (Goodyear, 1977a; McFadden and Lawler, 1977; Christensen et al., 1977; Fletcher and Deriso, 1988; Lawler, 1988; Savidge et al., 1988). Most of these models are based on the Ricker formulation and assume that the survival or reproduction of remaining individuals will increase in response to CWIS losses. It is thought

that this will enable the population to offset or compensate for CWIS-related mortality (Jude et al., 1987a; R.G. Otto & Associates and Science Applications International Corporation, 1987; Saila et al., 1987; Systec Engineering, Inc., 1987).

In a recent paper prepared for the Utility Water Act Group for the § 316(b) rulemaking, Myers (2001) noted that the life stage at which power plant mortality occurs in relation to the timing of any compensatory response will strongly determine the degree of impact. If compensation operates in a population and power plant mortality occurs before compensation, the impact on equilibrium spawner biomass and fishery yield may be small. However, if power plant mortality occurs after compensation on juveniles, there can be a more rapid decrease in equilibrium spawner biomass with plant mortality.

While such models can make general predictions, in practice they are limited in their ability to estimate the actual degree to which potential compensatory processes may enable any particular population to offset intake-related losses, as discussed in the following section.

A6-4 UNCERTAINTY IN STOCK-RECRUITMENT MODELS

A recent extensive review of available spawner-recruit data for commercially harvested marine fish stocks indicated that the recruitment of many exploited species shows a compensatory response to spawning stock (Myers et al., 1995; Myers and Barrowman, 1996; Myers et al., 1999). Data also indicate that compensation in fish species usually occurs during early life stages, although the exact timing varies by species and type of waterbody (Myers and Cadigan, 1993).

Although many fish species appear to show the potential for a compensatory response to changes in population size, in other cases a statistically significant density dependent relationship cannot be detected because of significant variability in the available population data (Shepherd and Cushing, 1990; Fogarty et al., 1991). For example, although there is a reasonably good fit of the Beverton-Holt and Ricker curves to data for coho salmon (Figure A6-5a), population data for anchoveta show considerable variation about the hypothetical stock-recruitment curves (Figure A6-5b).

Figure A6-5: The Ricker Curve (solid line) and Beverton-Holt Curve (dotted line) Fitted to Data for (a) Coho Salmon and (b) Anchoveta
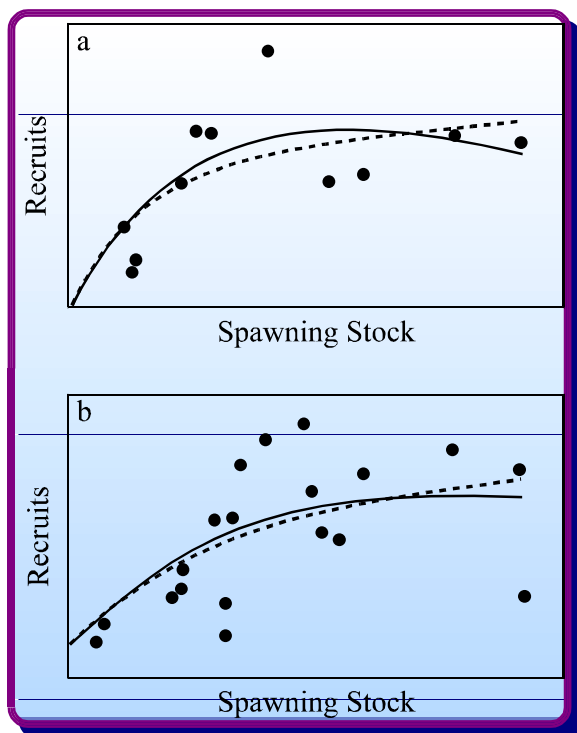
Source: Modified from plots by Kimmerer, 1999, of data compiled by Myers et al., 1995.

Two major sources of recruitment variability in fish populations can cause any compensatory relationship between spawning stock and recruitment to vary unpredictably in ways that are difficult to observe and measure. These are variation in the physical environment due to fluctuations in climate and other natural conditions (Cushing, 1982; Fogarty et al., 1991) and interactions with other species (Boreman, 2000).

Competition and predation can interact in complex ways with other sources of mortality to alter stock-recruitment relationships. For example, a model of trophic dynamics among fish populations in the Patuxent River that are subject to harvesting as well as CWIS impacts predicted a significant reduction (over 25%) in striped bass, bluefish, and weakfish production as a result of power plant losses of preferred prey species such as bay anchovy and silversides (Summers, 1989). Thus, CWIS losses can contribute to reduced overall ecosystem productivity, irrespective of any potential compensation in populations directly affected by CWIS mortality (Boreman, 2000).

Most existing CWIS stock-recruitment models do not consider:

- ▸ Losses of more than one species,
- ▸ Losses from multiple CWIS,
- ▸ Other human-related sources of mortality (in addition to fishing and CWIS),
- ▸ Interactions among species, and
- ▸ Interactions among density-dependent and density-independent processes.

In practice the use of stock-recruitment curves to set fishing levels, or to determine how much I&E a population can withstand, is complicated by the many physical and biological factors that can cause the stock-recruitment relationship and potential compensatory reserve to vary over time (Christensen and Goodyear, 1988; Cushing, 1982; Fogarty et al., 1991; Boreman, 2000). It is now acknowledged that fish recruitment is a multidimensional process, and separating the variance in recruitment into its component causes remains a fundamental problem in fisheries science, stock management, and impact assessment (Hilborn and Walters, 1992; Quinn and Deriso, 1999).

Because the relationship between spawners and recruits may itself vary, applying fixed rules for achieving constant fisheries yields or taking of young by cooling water intakes can have very different effects, depending on whether population size is high or low (Clark, 1990; Myers et al., 1996).

Even if compensation operates, if and how quickly a population can recover from anthropogenic sources of mortality depends on the population's growth rate at low densities (Liermann and Hilborn, 1997; Myers et al., 1999; Liermann and Hilborn, 2001). As the degree of compensation or age at recruitment declines, there can be a dramatic reduction in the level of fishing or other anthropogenic mortality that a population can sustain (Mace, 1994). When a population at low abundance continues to be reduced by a fixed amount, the population may gradually lose resilience and may suddenly collapse in the face of disturbances that previously could have been assimilated (Goodyear, 1977a; Holling, 1996). If exploitation levels or other stressors remain high during the decline, recovery may be protracted, if it occurs at all (Fogarty et al., 1992). In the case of the winter flounder in Mt. Hope Bay, Massachusetts, substantial population decline has been associated with both overfishing and mortality associated with the operation of the Brayton Point facility (Gibson, 1996). Even though fishing restrictions have been imposed, the population has failed to recover in the face of ongoing power plant mortality.

A6-5 PRECAUTIONARY APPROACH

Some industry representatives have argued that the environmental impacts of CWIS are adverse only if population-level impacts are demonstrated. These groups argue that compensatory processes help maintain stable fish stocks despite CWIS losses in most, if not all, affected populations. However, EPA is concerned that even in fish populations where compensatory processes are thought to operate, it has proven extremely difficult to estimate the magnitude of compensation and the form of compensatory response (Rose et al., 2001). This is a particular concern for commercially exploited marine species. A recent report by the National Marine Fisheries Service concludes that nearly a third of the 283 fish stocks under U.S. jurisdiction are currently below their maximum sustainable yield (NMFS, 1999b). For another third, the maximum sustainable yield remains uncertain. EPA notes that many of these stocks are also subject to impingement and entrainment losses.

Given that many fish stocks are at risk, EPA has adopted a "precautionary approach" in evaluating CWIS impacts because of the many uncertainties associated with modeling compensation and stock-recruitment relationships. As practiced by many natural resource agencies, the precautionary approach aims to prevent irreversible damage to the environment by implementing strict conservation measures even in the absence of unambiguous scientific evidence that environmental degradation is being caused by human stressors (NMFS, 1999b).

In this regard, many agencies now recognize that if protective measures are not initiated until effects at higher levels of biological organization are apparent, natural resources that are ecologically important or highly valued by society may not be adequately protected. In the context of the § 316(b) rulemaking, EPA notes that most CWIS cause substantial losses of aquatic organisms, and EPA believes that it is not appropriate to assume that these impacts are unimportant unless population-level consequences can be demonstrated. EPA notes that in other cases where a stressor directly affects individuals but population or higher-level effects are unclear though potentially important, individual-level endpoints often take precedence when evaluating environmental impacts (Strange et al., 2002). Indeed, in many Clean Water Act (CWA) programs EPA has found that effects on individuals can be important predictors of potential effects on populations or communities that can't be measured directly.

An example of this is provided by the National Pollutant Discharge Elimination System (NPDES) permit program. Under section 301(b)(1)(c) of the CWA, effluent limits must be placed in NPDES permits as necessary to meet water quality standards. To implement this requirement, EPA and most states rely on toxicity tests that determine the effects of discharges on individual organisms (U.S. EPA, 1991). By evaluating the effects of pollutants on growth, reproduction, and mortality of individuals, EPA uses individual impacts as surrogates and precursors of population and ecosystem impacts.

For the § 316(b) benefits case studies, EPA has chosen to evaluate multiple endpoints, including the impingement and entrainment of individuals, the most direct measures of CWIS impact. In addition, to evaluate the potential population-level consequences of these losses for economically valued endpoints, EPA has implemented several density independent models to conservatively estimate potential consequences for fishery harvests and ecosystem production, as described in detail in Chapter A5. These density independent models do not assume any compensatory response to CWIS losses. While relationships between CWIS losses, fish stocks, and fishery yields are unlikely to be strictly linear, as these models assume, EPA believes that the many uncertainties associated with modeling stock-recruitment relationships and potential compensation justify this approach, in keeping with a precautionary approach to environmental decision-making.